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Ecology and Evolution of Snake Mating Systems

David Duvall

Gordon W. Schuett

Stevan J. Arnold

Introduction

A goal of evolutionary behavior analysis is to predict strategies and other actions of animals. Indeed, given an appropriate model organism, were an investigator to have a substantive understanding of its overall biology, one could, in theory, even predict accurately the behavioral strategy that would maximize reproductive success. Some of the elements that would comprise such a complete understanding for a population or taxon might include knowledge of (1) comparative phylogenetic relations and relevant trait derivation (Brooks and McLennan, 1991; Harvey and Pagel, 1991), (2) phylogenetic inertia manifested in proximate characteristics (including life-history patterns and more unitary adaptations; Seigel and Ford, 1987; Shine, 1988a; Harvey and Pagel, 1991; Duvall et al., 1992; Stearns, 1992), (3) the current panorama of variance in relevant trait values (Endler, 1986; Harvey and Pagel, 1991), (4) local ecological potential favoring some actions and strategies and not others (Orians, 1969; Emlen and Oring, 1977; Alcock, 1980; Thornhill and Alcock, 1983; Davies, 1991), (5) current natural selection forces (Endler, 1986), (6) current sexual selection forces and mating-system characteristics (Bateman, 1948; Wade, 1979; Wade and Arnold, 1980; Arnold, 1983; Arnold and Wade, 1984a,b; Bradbury and Andersson, 1987), and (7) relevant trait heri-

tabilities (Lande, 1979; Arnold, 1983; Brodie and Garland, Chap. 8, this volume). Obviously, however, much more needs to be learned about the main effects and interactions of these many forces and variables in order to achieve a more precise predictability about reproductive strategy.

This is not to say that exciting progress on these many fronts has not been made, progress that allows good predictability even with much remaining to be learned. Particularly exciting progress has been made in the areas of sexual selection and mating-system analysis, headway germane to this chapter. And even though snakes only recently have become a focus of active research in this area, this dearth of knowledge about mating systems and sexual selection is bound not to last. Our own field (Graves and Duvall, 1990; Duvall et al., 1992), laboratory, and theoretical work (Duvall et al., 1992; Schuett, 1992; Arnold and Duvall, 1993) suggests potentially fruitful directions and possibilities for the analysis of snake mating systems and sexual selection patterns. Thomas Madsen, Richard Shine, and several other investigators (Gregory, 1974; Andr n, 1986; Slip and Shine, 1988a; Madsen et al., 1992; Shine, Chap. 2, this volume) now are making significant contributions in this area as well.

In this chapter we continue our dialogue on sexual selection, male and female strategy, and pattern and variation in mating systems, though in this chapter we broaden our focus to include snakes more generally. As in previous contributions, we focus primarily upon mating systems and sexual selection in the context of (1) local ecological potential and (2) phylogenetic inertia for certain mating-system patterns and not others (see Fig. 5.1). We also provide a treatment of some potential methodological approaches and kinds of data that

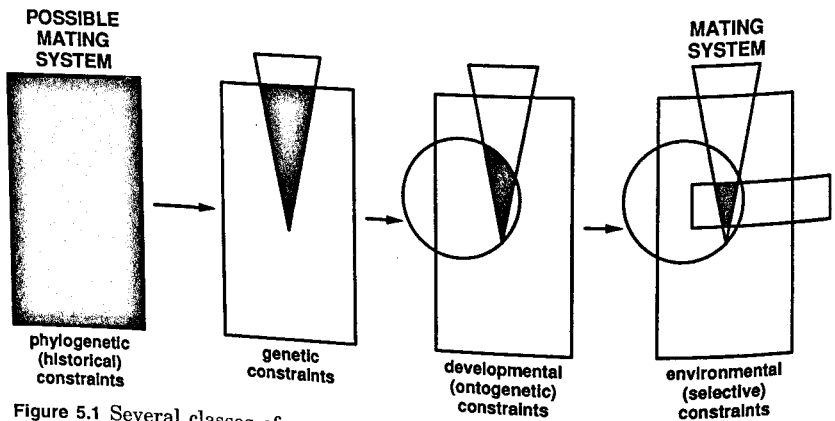


Figure 5.1 Several classes of constraints presumed to shape the ultimate form of an hypothesized, realized mating system. From Schuett and Duvall (unpub.). Modified from Brooks and Wiley (1988).

might be gathered were one to desire to work in this area. In the last major section of this chapter we survey some benchmark studies of snake reproductive biology that, in some instances, have a good deal to say about mating systems and/or sexual selection in snakes.

Theoretical and Conceptual Context

Though we do not wish simply to restate our theoretical propositions and reviews presented elsewhere (Duvall et al., 1992; Arnold and Duvall, 1993), nor review the voluminous, relevant general theoretical and empirical literature (Darwin, 1871; Bateman, 1948; Trivers, 1972; Emlen and Oring, 1977; Wells, 1977; Parker, 1978a,b; Shine, 1978; Howard, 1979; Payne, 1979; Wade, 1979; Alcock, 1980; Kluge, 1981; Andersson, 1982; Arnold, 1983; Thornhill and Alcock, 1983; Thornhill, 1986; Bradbury and Andersson, 1987; Shields, 1987; Clutton-Brock, 1988, 1989; Clutton-Brock and Vincent, 1991; Sullivan, 1989, 1991; Shine, Chap. 2, this volume) some treatment is necessary to provide context for one of our larger goals for this chapter, namely, reviewing and analyzing snake mating systems in abridged historical, theoretical, and empirical context. A second goal is to suggest directions for future study with descriptions of an approach and the kinds of data that might be utilized. The sample protocol we develop in next to the last section of this chapter would take advantage of potentially powerful DNA fingerprinting methods (Burke, 1989; Kirby, 1990). Refer to Table 5.1 for a list of variables mentioned throughout the text.

Sexual selection and mating systems

Though not always explicit in all treatments of mating systems, it is difficult not to consider simultaneously sexual selection forces in the context of reproductive strategy, whether they be intra- or intersexual, and whether these forces be greater on males or females. We (Duvall et al., 1992; Arnold and Duvall, 1993) have proposed that one good way to get a handle on symmetry or lack thereof in sexual selection forces acting on males and females in populations is to determine and compare sexual selection gradients for both males and females. We have defined these as the average slope of the partial regression of fecundity on mating success for members of each sex (see Fig. 5.2). The partial regression of fecundity on mating success must, by definition, simultaneously represent the final common pathway for all sexual selection forces. Thus mating success is more precisely definable as the *number of ego's mates that actually bear progeny* (see Arnold and Duvall, 1993). Accordingly, members of that sex in a population with the steepest sexual selection gradient will be those experiencing

TABLE 5.1. Variables Comprising Mating System and Related Models

Variable	Definition
\bar{m}_f	Average fitness (= fecundity or progeny count) of all females
\bar{m}'_f	Average fitness of females that mate once or more
\bar{m}_m	Average fitness of males
\bar{X}_f	Average female mating success (= number of mates)
\bar{X}_m	Average male mating success
H_x	Harmonic mean mating success of females with one or more mates
σ^2_{x-f}	Variance in mating success for all females (including the zero class with no mates)
σ^2_{x-m}	Variance in mating success for all males
q	Female mating failure (proportion of females capable of breeding that do not) (note that $p + q = 1$)
β_{ss-f}	Female sexual selection gradient
β_{ss-m}	Male sexual selection gradient
OSR	Operational sex ratio (the average over time of the number of sexually active males to the number of females capable of insemination)
BSR	Breeding sex ratio (= parental ratio; ratio of number of breeding males to number of breeding females)
L	Length of mating season
s	Mate searching time
h	Mate handling time
c	Mate cycling time (= $s + h$)
α_s	Average mate searching time
α_h	Average mate handling time
α	Average mate cycling time (= $\alpha_s + \alpha_h$)
α_p	Average mate persuasion efficacy
$\beta_{ss-\alpha_s}$	Sexual selection gradient for average searching time
$\beta_{ss-\alpha_h}$	Sexual selection gradient for average handling time
$\beta_{ss-\alpha}$	Sexual selection gradient for average mate cycling time
$\beta_{ss-\alpha_p}$	Sexual selection gradient for average mate persuasion
σ^2	Variance in mate cycling time
σ^2_p	Variance in mate persuasion efficacy
I_s	Potential for sexual selection (variance in mating success standardized to a mean of 1; = σ^2/\bar{x}^2)

the most intense sexual selection on traits associated with the mating-success-fitness-regression slope. Conversely, that sex with the relatively flatter sexual selection gradient will realize a smaller relative gain in fecundity as a function of continued matings, because selection on traits associated with mating success per se is less. In a very real sense, this explanation for inherent sex differences, based upon a determination and calculation of male and female popula-

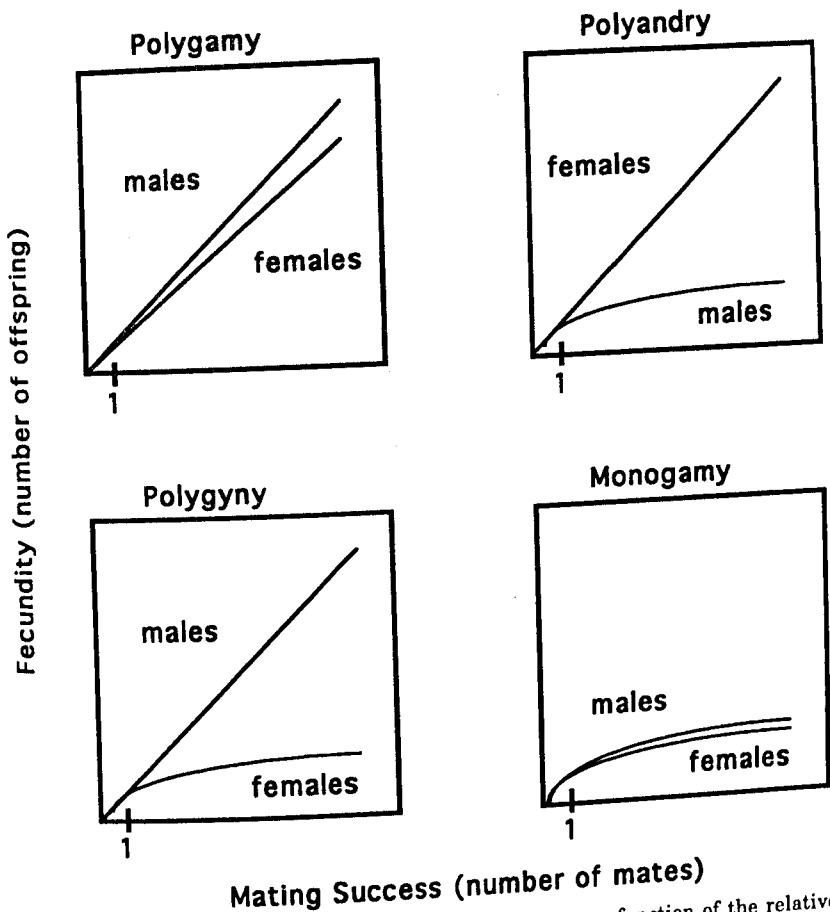


Figure 5.2 Predicted, broad sense mating-system types as a function of the relative association of fecundity and mating success for males and females. We term these associations sexual selection gradients. Modified from Arnold and Duvall (1993). See text for additional discussion.

tional sexual selection gradients, is a fresh explanation for proximate differences for male and female differences in sexual strategy. Most popular explanations focus on the ultimate origins of differences in sexual strategy, rather than on actions of sexual selection in progress on key proximate traits [compare Bateman (1948), Arnold and Wade (1984a,b), and Arnold and Duvall (1993), with Trivers (1972), Borgia (1979), Thornhill (1986), and Gwynne (1991)].

An advantage of our framework for mating systems and sexual selection analysis is that it provides an integrated, quantitative system that focuses upon empirically tractable parameters. Less specific and nonintegrative approaches, many of which include as the domain of mating-system analysis almost everything about the reproductive

and mating biology of natural populations of animals, in fact may predict less.

We also advocate construction of a "parental table" (Arnold and Duvall, 1993), which comprises an empirical sampling of individual male and female parents of an acceptable sample of offspring in a target population. Such data represent the most direct method of determining precisely the relative male and female sexual selection gradients characteristic of a population. These data also would allow determination of the breeding sex ratio (BSR), or the ratio of actual male to female parents, which can provide an accurate index of sexual selection forces acting within populations (Duvall et al., 1992; Arnold and Duvall, 1993). Because each and every individual offspring in a population can have only two parents, the BSR reflects all such sets of parents and provides a quantitative index of the degree of constraint each sex places over the reproductive success of the other. Though we have also modeled conditions whereby behavioral data can be used to determine both the BSR and parental table (see below), protein electrophoresis and DNA fingerprinting data would be ideal (Gibbs et al., 1990). Indeed, the accuracy of the operational sex ratio [OSR, the ratio of potential mothers to fathers in a population, though we and most others cast this oppositely (see Table 5.1); Emlen and Oring, 1977] may lie in the extent to which it predicts the BSR. The OSR is often taken as a predictor of intrasexual competition and even sexual selection forces (Emlen and Oring, 1977), and relies heavily on the importance of female-mate monopolization potential. OSR theory predicts, for example, that male-biased OSR and increased male mating competition will be associated positively with increasing potential sexual selection forces acting on males. However, Ims (1988) has shown that female-biased OSRs, more so than male-biased OSRs, are more predictive of increased variance in male mating success. Ims' (1988) findings thus run counter to OSR theory, and appear to hold for mating systems akin to those seemingly more characteristic of snakes, and, interestingly, many mammals (Ims, 1988), namely those characterized by mate searching, guarding, and male fighting. OSR may, however, be more predictive of mating competition in territorial-type and perhaps hotspot mating systems (Arnqvist, 1992; see below). However, we know of no reports *confirming* territoriality in snakes (see below). See Duvall et al. (1992) and Arnold and Duvall (1993) for additional discussion.

Though perhaps only indirectly germane to analyses of snake mating systems, at least given our present knowledge of snake reproductive patterns and strategy in nature, nuptial gifts and parental care also can change the slope of sexual selection gradients, reflecting changing potential sexual selection forces. Arnold and Duvall (1993) take up these and related issues.

Kinds of mating systems: Broad and narrow senses

Arnold and Duvall (1993) present a quantitative scheme that holds some potential for analyzing and even classifying diverse animal mating systems (see Fig. 5.2). Two of the systems therein seem germane to snakes, especially *polygyny* and, to a lesser extent, effective *monogamy*. As we define it, in a polygynous snake mating system males realize increased fecundity with increased mating success. Females, conversely, experience an asymptotic fecundity curve because increased mating success will not increase fecundity. The road to female snake reproductive success instead will be paved with elements of efficacious foraging and feeding, and efficient energetic biology and pregnancy or gestation. This no doubt is due to the relatively extreme energetic costs per potential egg or offspring experienced by most female snakes, which greatly reduces their theoretical lifetime reproductive potential. Duvall et al. (1982, 1990, 1992) and Graves and Duvall (1990, 1993) take up these and related issues (see also Shine, 1988b). Accordingly, we should not be surprised as well to discover more robustness and variation in maternal investment adaptations among female snakes (Shine, 1988b; Graves and Duvall, 1993). Arnold and Duvall (1993), for example, find that maternal care of clutches or litters will decrease sexual selection forces acting on females.

When matings with multiple females are unlikely, for whatever reason(s), effective monogamy seems possible. This would be recognized in our system by roughly similar, asymptotic male and female partial regression slopes for fecundity and mating success. We imply nothing about pair bonding, or other proximate behavioral mechanisms that may mediate sustained gregariousness of male-female pairs. It is also relevant here that male snakes are largely unable to capture and supply food to pregnant or gravid females, by virtue of snakes' feeding biology and general morphology (see Duvall et al., 1992 for additional discussion).

Finally, because of the phylogenetic momentum for polygyny among the snakes, neither polyandry nor polygamy as defined in Fig. 5.2 are likely to occur.

It is appropriate, therefore, to consider the scheme diagrammed in Fig. 5.2 as providing a *broad sense* classification of potential snake or animal mating systems. More *narrow sense*, but less general, classifications would seem to fall naturally under the four broad sense rubrics portrayed in Fig. 5.3. Under polygyny and focusing on snakes, for example, and employing accepted narrow sense classifications such as the proven and popular scheme of Thornhill and Alcock (1983; see also Emlen and Oring, 1977; Bradbury et al., 1986), Duvall et al. (1992) describe and predict at least four forms of polygyny that,

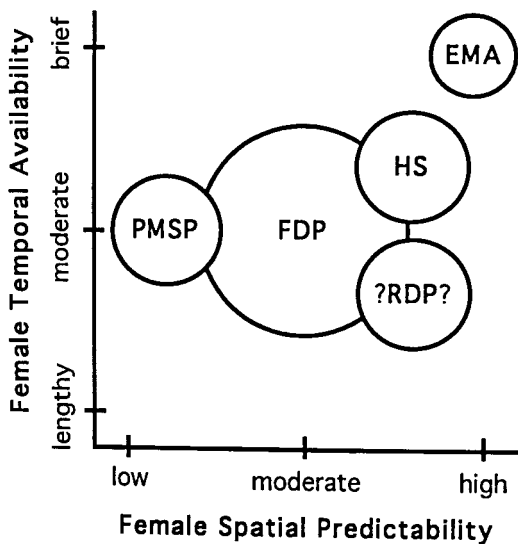


Figure 5.3 Some hypothesized, narrow-sense mating-system types, which, for most snakes, should fall under the rubric of polygyny. Circles and their areas are hypothesized to reflect the extent to which one or another form of polygyny should be expected, as a function of receptive female spatial and temporal predictability. FDP is female defense polygyny, or mate-guarding, and is probably very common among snakes. PMSP is prolonged mate-searching polygyny, EMA is explosive mating assemblage, and HS is hotspot polygyny. The entry for RDP, resource defense polygyny or territoriality, is qualified with question marks because it has yet to be demonstrated unequivocally in snakes. See text for additional discussion.

were they found to occur, may cover the gamut of types of snake mating systems (see Fig. 5.3). These subtypes of polygyny are predicted to be determined by distributions of receptive females both in time and space, and, thus, by similar distributions of resources important to females (Duvall et al., 1992). Again, a problem with narrow sense approaches is that they are somewhat idiosyncratic and not especially general.

Nevertheless, in the narrow sense, the four common snake mating systems likely are (1) female defense polygyny, or mate guarding, (2) hotspot polygyny (Bradbury et al., 1986), (3) prolonged mate searching polygyny, and (4) explosive mating assemblage. The latter two mating system types commonly are considered to be subcategories of scramble competition polygyny (Thornhill and Alcock, 1983). Territoriality, or resource defense polygyny, and Lek polygyny are, at present, unknown or unsubstantiated in snakes. Leks are male dis-

play areas where females may choose mates. The key test for those who are interested in the potential of territoriality in snakes will be to demonstrate that males compete for control of resources, habitats, and the like, that, in turn, are important to and/or selected by females. To show male-male fighting and competition in the presence of one or more receptive females, for example, is not sufficient. We expand upon this important issue below. Finally, we find little use for terminology and classification systems that are specific to one sex and that do not consider simultaneously symmetry and departures from symmetry that characterize strategy for both sexes (and on this one count we depart from Thornhill and Alcock, 1983).

As noted above, a variant of the hotspot polygynous mating system (Davies, 1991) may occur in some snakes (see below). Such a mating system would probably represent yet another subtype of scramble competition polygyny, where males move to and gather in locales where females are relatively abundant, the latter presumably occurring there in response to some limiting environmental feature, such as warmth or food, for example. Male-male fighting and even mate guarding of females may or may not occur in such locales (see below). However, we invoke nothing regarding potential female choice in hotspots, a component of initial formulations of this idea. We apply it here only to help explain relative spatial overabundance of receptive females in a locale or habitat unit.

A related and significant variable affecting any form of male-male competition that might occur in hotspots would be the phenomena of female multiple mating and mixed paternity, sperm competition and storage, and any mating-order effects on male fertilization success that may exist (Parker, 1970a, 1984; Dewsbury and Baumgardner, 1981; Devine, 1984; Schwagmeyer et al., 1987; Schwartz et al., 1989; Schwagmeyer, 1990; Schuett, 1992). For example, if females mate multiple times, if paternity is mixed, if no mating-order effects exist, if no physiological mechanisms (e.g., Garter Snake mating plugs; Devine, 1977) exist to enforce chastity or single male matings, and if the duration of female receptivity is even moderately lengthy, it is expected that males at a female hotspot will *not* fight. Rather, we might expect these hypothetical males simply to queue up and wait their turn. We expand upon this issue below.

Aside from effective female choice of males via potential sperm competition and mixed paternity of broods or litters, a suite of reproductive adaptations probably characteristic of many snakes (see Schuett, 1992), no reports currently exist indicating active, behavioral choice of mates by females. However, Schuett and Duvall (in review) discuss what may represent the first report of female mate choice among snakes (see below). Nevertheless, sexual selection

among most snakes probably derives from various forms of male-male competition.

Sexual selection gradients, encounter rate theory, and mating systems

As noted above, the sexual selection gradient context for most snake mating systems is polygynous, as portrayed generally and graphically in Figure 5.2. This diagram tells us that, for many or most snake mating systems, males generally will realize increased fecundity with successively numerous matings but that females will not. Selection for traits boosting mating success therefore will have its greatest impact upon males rather than on comparable traits of females, and, thus, polygyny among snakes. Duvall et al. (1992) discuss in detail additional reasons for polygyny among snakes.

We can formalize this general situation in ways that allow us to study predictively polygynous snake mating systems and sexual selection. For purposes of theoretical development, we focus now only on selection operating within single seasons, with no formal accounting of population age-structuring and complex life histories. Arnold and Duvall (1993), however, do discuss mating systems in the context of age-structuring and mortality.

We begin by imagining a mating system in which males garner increased fecundity from multiple matings, but females do not (Fig. 5.4). Such a circumstance bears good resemblance to the reproductive functioning of most male and female snakes (Duvall et al., 1982, 1992; Schuett, 1992), and facilitates formal modeling that should further empirical analyses (Duvall and Schuett, in review). If a female mates once or more, her average fecundity equals some constant, say \bar{m}'_f and is zero if she mates not at all. The average for all males in the population, both mated and unmated, is \bar{m}_f . Suppose that p is the proportion of females capable of breeding that mate once or more and bear progeny, and q is the proportion of females capable of breeding that do not mate ($p + q = 1$), then the average fecundity of females mating one or more times is

$$\bar{m}'_f = \bar{m}_f/p. \quad (1)$$

Females of many snake taxa long have been suspected of multiple mating (Madsen et al., 1992; Schuett, 1992), sperm storage, and probably competition, as well as mixed paternity of clutches or litters (Ludwig and Rahn, 1943; Gibson and Falls, 1975; Saint Girons, 1975; Devine, 1984; Schuett, 1982, 1992; Schwartz et al., 1989). It is unknown, however, if any mating order effects arise from multiple matings among snakes. Nevertheless, if the number of progeny an individual male can expect to sire is inversely proportional to the

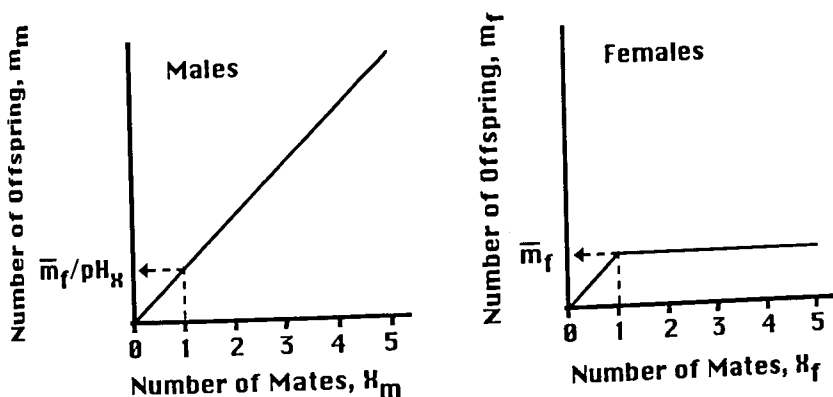


Figure 5.4 Model sexual selection gradients for a polygynous mating system, probably characteristic of most snakes, wherein average male fecundity (\bar{m}_m) does, but average female fecundity does not (\bar{m}_f), increase beyond that derived from the first mating. However, for taxa or populations with multiple sires, mixed paternity of clutches or litters, and no mating order effects, yet another system probably characteristic of many snakes, average male fitness is given by \bar{m}_f/pH_x , where p is the proportion of females that mate once or more and bear progeny and H_x is the harmonic mean number of male mates per female. See text for discussion. See also Arnold and Duvall (1993) and Duvall et al. (1992). Modified from the latter.

number of different males a target female actually mates with, then expected male fitness \bar{m}_m is

$$\bar{m}_m = \bar{m}_f \bar{X}_m / pH_x, \quad (2)$$

where H_x is the harmonic mean mating success of females with one or more mates (Fig. 5.4). Thus, \bar{m}_m is inversely proportional to the harmonic average number of different males mated by an individual female.

As discussed by Duvall et al. (1992) and Arnold and Duvall (1993), by taking the first derivative of average male fecundity with respect to average male mating success, we find that the sexual selection gradient for males (β_{ss-m}) in the single male paternity system (i.e., where $H_x = 1$) is

$$\beta_{ss-m} = \bar{m}_f / p. \quad (3)$$

In a system characterized by multiple female mating and mixed paternity this gradient becomes

$$\beta_{ss-m} = \bar{m}_f / pH_x. \quad (4)$$

Thus, in the absence of other effects, multiple mating by females coupled with multiple paternity is expected to reduce the force of sexual selection on males.

For purposes of symmetry, and not because sexual selection gradi-

ents among females of any snake taxa are expected to be steeper than those of conspecific males (Duvall et al., 1992; Arnold and Duvall, 1993), it is useful to consider those parameters affecting sexual selection gradients for females (β_{ss-f}). This relationship is more complex among females, and is given by

$$\beta_{ss-f} = q\bar{m}_f \bar{X}_f / p\sigma_{x-f}^2, \quad (5)$$

where q is an index of female mating failure, or the proportion of females capable of breeding that do not, \bar{X}_f is the average mating success of all females, and σ_{x-f}^2 is the variance among all females in mate number (including the zero class with no mates). Thus, so long as there is some variance in female mate numbers, mating failure is a prime factor promoting sexual selection in females. However, it is expected that among most female snakes mating failure should be minimal, which means that q will be small and β_{ss-f} will approach zero. This was, for example, in fact the case in our long-term field study of Prairie Rattlesnakes (Duvall et al., 1992; Duvall and Schuett, in review; see below).

Encounter rate phenomena and sexual selection gradients

Clearly, it would be useful to have available some means of extending formally sexual selection and mating systems theory in an empirically tractable fashion, whether a student of snakes were working in the laboratory or field. Next we describe some readily studied behavioral and phenological parameters, that may make possible a connection between relevant selection theory and behavioral empiricism. Again, consult Duvall et al. (1992) and Arnold and Duvall (1993) for additional information.

Like others (Holling, 1959; Parker, 1970a,b, 1974, 1978a,b; Baylis, 1981; Sutherland, 1985a,b, 1987; Real, 1990), we find it convenient and empirically tractable to cast key seasonal, behavioral, and reproductive phenomena in terms of accumulated time per activity and rates (Duvall et al., 1992; Arnold and Duvall, 1993). This is because encounter rate phenomena are easily observed and scored, a relevant body of renewal theory exists (Cox, 1962), some of which we employ below, and relevant data lend themselves nicely to statistical analysis (Duvall et al., 1992; Arnold and Duvall, 1993). The path diagram portrayed by Fig. 5.5 provides a fitness-related context in which such information can be considered.

We begin by defining arbitrarily distributed and statistically independent mate searching (s) and handling (h) time as key parameters. Furthermore, each round of s and h sum to accumulated mate cycling

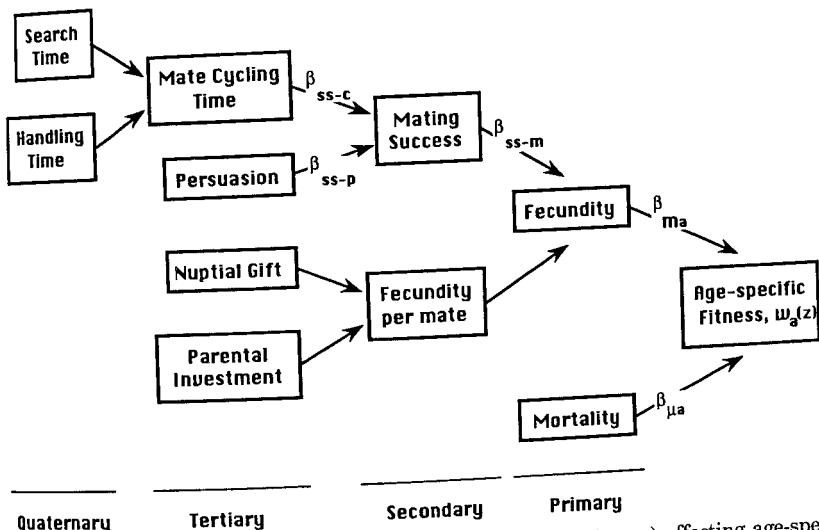


Figure 5.5 A hierarchy of traits (quaternary down through primary) affecting age-specific fitness [$w_a(z)$], with special focus on those descending to mating success. The symbols along respective paths denote selection coefficients known as selection gradients (β values) and are discussed either in the text or in Arnold and Duvall (1993). Modified from Arnold and Duvall (1993). See text for additional discussion.

time (c) per potential mating ($c = s + h$). There may be few or many reproductive periods c per discrete reproductive period or season. Reproductive periods or seasons are of duration L , and there may be few or many of these as well. There may be one or several such periods L per year or season, depending on the taxon or population in question, and males and females may have different mate-cycling-time profiles. Handling includes activities such as mate accompaniment, courtship and copulation, mate guarding, male-male fighting, and the like. Period L is comprised entirely of searching and handling ($s + h$); in other words, once a unit of mate cycling time c is completed, whether or not a successful copulation results, another period c commences immediately. In our various studies of snake mating systems, where one focus has been variance in male fighting (= handling; Schuett and Duvall, in review) and male mate searching (Duvall and Schuett, in review), we “debit” and “credit” winners and losers of fights over potential mates, respectively, with appropriate negative increments of handling time h . Mate search failure likewise can be dealt with as a negative debit to accumulated search time. Such parameters also could be studied in the laboratory (see below). Additionally, since not all mates encountered will be independent measure of proportional mate persuasion efficacy p . Accordingly, we also can define means and variances for these parameters, and

these are for c , s , h , and p , (1) α and σ^2 , (2) α_s and σ_s^2 , (3) α_h and σ_h^2 , and (4) α_p and σ_p^2 , respectively. Because of our assumption of independence, it follows that $\alpha = \alpha_s + \alpha_h$ and $\sigma^2 = \sigma_s^2 + \sigma_h^2$.

Focusing on males, as in Duvall et al. (1992) and Arnold and Duvall (1993), we find that average male mating success is

$$\bar{X}_m = \alpha_p L / \alpha. \quad (6)$$

Males thereby can increase mating success by (1) maximizing mate persuasion efficacy, (2) maximizing mating season duration, and (3) minimizing overall mate cycling time. Now, since variance in the number of mates cycled per season is $\sigma^2 L / \alpha^3$, as discussed by Cox (1962) and Arnold and Duvall (1993), variation in male mating success, σ_{x-m}^2 , is

$$\sigma_{x-m}^2 = (\alpha_p^2 L^2 / \alpha^2) \{ (1/\alpha L) \sigma^2 + (1/\alpha_p) \sigma_p^2 \}. \quad (7)$$

We assume that cycling time and mate persuasion are statistically independent. If we divide Eq. (7) by the square of mean mating success, $\alpha_p L / \alpha$, we obtain the standardized variance in relative mating success I , which is an index of the potential opportunity for sexual selection (Crow, 1958; Wade, 1979; Wade and Arnold, 1980; Arnold, 1986). We find that

$$I_{x-m} = (1/\alpha L) \sigma^2 + (1/\alpha_p^2) \sigma_p^2. \quad (8)$$

Accordingly, the opportunity for sexual selection is increased by (1) high variances in cycling time and persuasion, (2) brief average cycling time, (3) a short mating season, and (4) low average persuasive ability. Moreover, while the effects of short average cycling time and breeding season duration are to enhance the contribution of variance in cycling time to the opportunity for sexual selection, low average persuasion has the same effect on variance on this same parameter. And, as discussed by Arnold and Duvall (1993), since we can define the relative variance in number of mates cycled to be the ratio of absolute variance in numbers cycled to the squared mean number of cycled mates, $I_c = \sigma^2 / L\alpha$, and the relative variance in persuasion to be $I_p = \sigma_p^2 / \alpha_p^2$, then Eq. (8) becomes

$$I_{x-m} = I_c + I_p. \quad (9)$$

The opportunity for sexual selection, therefore, is simply the sum of selection opportunities arising from mate cycling and persuasion activities. Arnold and Duvall (1993) discuss a few approaches that can be employed when significant covariance arises between numbers of mates cycled per season and persuasion efficacy.

Sexual selection gradients and encounter rate parameters. There also is utility in casting encounter rate parameters in terms of sexual selection gradients. By calculating the partial derivative of \bar{X}_m with respect to α , α_s , and α_h , we find that

$$\beta_{ss-c} = \beta_{ss-s} = \beta_{ss-h} = -\alpha_p L / \alpha^2, \quad (10)$$

and for α_p ,

$$\beta_{ss-p} = L / \alpha. \quad (11)$$

Sexual selection gradients for L and L/α likewise can be determined by calculating first derivatives using Eq. (6).

Consequently, sexual selection on male rates is expected to increase as (1) average persuasion abilities increase, (2) mating season duration increases, and/or (3) average mate cycling times decrease. Sexual selection should act on males to (1) increase persuasion capacities, (2) extend duration of mating seasons, and (3) decrease the duration of average mate cycling times. Generally, sexual selection on encounter rates will be most intense when $L \gg \alpha$, and when average persuasion efficacy is high.

Perhaps most importantly for students of snakes, these formulations suggest some testable predictions for those interested in snake mating systems and sexual selection. In snake mating systems characterized by fighting or mate guarding, or even complex courtship activities, for example, the models we provide surrounding handling time h provide a means for integrating the analysis of such behavior, whether in the lab or field, into formal evolutionary theory. The same is true for searching time s , though this parameter may be studied more effectively in the field. The BSR also has practical and empirical utility because it may be more predictive of dynamic sexual selection forces in a variety of circumstances, than the OSR. DNA fingerprinting approaches may be especially useful in studying the latter, as we describe in some detail just below. And finally, the variance formulations defined above suggest clear-cut pathways for studying behavioral, reproductive, and genetic variables that increase dispersion from the mean, and, thus, potential sexual selection forces across a broad range of relevant phenomena.

Measuring Sexual Selection Gradients in Snake Populations

The data required to address many of the conceptual issues that we have discussed could be obtained in some snake populations. In particular, the denning habit of some species (Klauber, 1936; Gregory,

1984; Graves and Duvall, 1990) offers an exceptional opportunity to capture and monitor the reproductive success of an entire local population. We will focus on the situation in which all (or virtually all) of the mating partners in a local area can be captured at one or more dens. The research program is easiest to visualize if we imagine capturing and monitoring every breeding adult in the population. Such total sampling may not be practical in an actual situation, and so some statistical issues may arise that we will not address. Let us first consider the sequence of steps in obtaining data and then a series of steps in data analysis.

Obtaining the data

1. Enclose a hibernaculum and capture all emerging snakes. Enclosures can be built over hibernaculum openings that will fence in the emerging snakes so that they can be captured for processing. A number of authors describe apparatuses of this nature (Klauber, 1972; Fitch, 1987).

2. Equip all females capable of breeding with radiotransmitters. The aim here is to be able to find the females when they are gravid at the end of the season, so that they and their offspring may be captured. The details of fitting snakes with radiotransmitters are discussed by numerous authors (Reinert, 1992).

3. Take tissue and/or blood samples from all males capable of breeding. The tissue samples are then frozen for later use in paternity analysis. This data step relies on the fact that in humans and apparently many vertebrate populations almost every individual has a unique number of copies of certain highly repetitive genes (Jeffreys et al., 1985). That copy number can be determined and used as a "DNA fingerprint" in paternity analysis (Vassart et al., 1987; Wetton et al., 1987; Burke, 1989; Westneat, 1990). Fitting each male with a passive integrated transponder (PIT) tag is an option that could also be implemented at den capture time. PIT tags are small (ca. 1×4 mm) glass cylinders (enclosing an integrated circuit) that can be injected into a snake's body cavity. The snake's PIT tag responds with a unique identification number when activated by a detector that is held close to the snake's body. It is feasible to automate the detection process, so that snakes crawling past a detector, as they enter the enclosed den opening at the end of the season, are automatically recorded. Such automated detection would enable the investigator to score male survivorship, if it is safe to assume that a snake that fails to return is dead. Survivorship is an important issue in analyzing reproductive success in species that mate away from the den, because we will need to know which males were alive throughout the mating season.

4. Locate and capture all breeding females and their offspring. The period of egg-laying or birth lasts only a few weeks each year in many snake species. Consequently, the search for gravid females can be scheduled before the onset of the laying or birth season. Finding the females would be greatly facilitated by radiotransmitters. In some species (e.g., of *Thamnophis*, *Crotalus*) gravid females aggregate (Duvall et al., 1985; Huey et al., 1989; Graves and Duvall, 1993). In such species a good sample of gravid females can sometimes be obtained even without radiotransmitters. Even if only a few females are fitted with radiotransmitters, they may greatly help in locating female aggregations. The aim in capturing gravid females is to determine their brood sizes and obtain tissue from their progeny so that paternity analyses can be undertaken. One of us (S.J.A.) has had good success obtaining broods of natricine snakes (*Thamnophis* and *Nerodia*) by transporting gravid females to the laboratory and maintaining them individually on thermal gradients for several weeks until offspring are born. In this way about 1500 broods were obtained over a 15-year period. Production line methods for egg-laying species have been developed by commercial snake breeders.

5. Obtain tissue samples from all mothers and newborn offspring. Blood samples could be obtained without killing mothers or offspring and the snakes could be released afterward. The liver is easily biopsied in *Thamnophis* (and presumably in other snakes) without killing the snake. It would be important to obtain tissue samples from all available offspring in each brood because of the possibility of multiple paternity.

6. Determine the paternity of all offspring (e.g., using DNA fingerprinting). Molecular techniques are discussed in Vassart et al. (1987), Wetton et al. (1987), and Kirby (1990), and data analysis is reviewed by Kirby (1990).

7. Construct the parental table. This table lists individual adult females as labels for its columns and individual adult males as labels for its rows. Each cell in the table (intersection of a row and column) gives the number of offspring produced by a particular male and female pair. If all the offspring that a population produced are represented in the table, then the row totals give the fecundity of each male and the column totals give the fecundity of each female. The parental table is a useful summary of the paternity analysis even though many cells in the table will contain zeros. In particular, non-breeding but adult animals of both sexes should be included in the table even though their rows or columns will be entirely composed of zeros. The inclusion of these animals is crucial because breeding failure is a potentially important component of some of the statistics of reproduction and sexual selection.

Analyzing the data

Although a formidable amount of effort would be required to execute the entire research program that we have outlined, a very large number of questions could be answered with such data. Several of these are listed next.

Measures of fecundity and mating success for each male and female. We have already discussed how we can obtain fecundity scores for individual males and females from the row and column totals of the parental table. Mating success scores also can be obtained by first making a revised version of the parental table. In this revised version we put a one in any nonzero cell and leave all the zero cells intact. To tally the mating success of any male (the number of mates that bore his progeny), we simply take the total for his row. Likewise, the mating success of any female is given by her column total.

Opportunities for selection in each sex mediated through fecundity and mating success. Opportunities for selection are simply standardized variances in fitness (or its components) that are useful because they place an upper bound on the magnitude of phenotypic selection (Crow, 1958; Arnold, 1986). For example, to compute the opportunity for fecundity selection in males, we calculate the variance in male fecundities (i.e., the variance of the row totals in the parental table) and divide this variance by the squared value of average male fecundity. The opportunity for sexual selection in males is computed by doing the analogous operations on the revised parental table. Selection opportunities for females are computed in the same way, using column totals. Arnold and Wade (1984a,b) discuss how the opportunity for fecundity selection in males can be partitioned into two parts: an opportunity for sexual selection (computed as discussed above) and a selection opportunity arising from variation in the average number of progeny per mate.

Sexual selection gradients for both sexes. To estimate the sexual selection gradient for males we compute an ordinary regression of fecundity (row totals from the parental table) on mating success (row totals from the revised parental table). In other words, treating fecundity as the Y variable and mating success as the X variable, we compute the regression slope for the least-squares line that predicts Y from X . This slope is our estimate of the male sexual selection gradient. The female sexual selection gradient is estimated in the same way, but using column totals instead of row totals from the parental tables. Arnold and Duvall (1993) give an example of such an analysis, using Bateman's (1948) published data.

Sexual selection gradients and fecundity selection gradients for various traits (determinants of fecundity and mating success). One can attempt to unravel the causes of variation in fecundity and mating success by measuring multiple traits and asking whether they are determinants of reproductive success. The exercise is statistical and statements about causation are merely inference. Lande and Arnold (1983) discuss the application of multiple regression to this problem and show how the resulting slope estimates correspond to coefficients of selection that appear in equations for evolutionary change. Imagine that we have measured a set of traits on each of the males and females whose reproductive success has been assessed. Body size, tail length, head width, and other sexually dimorphic attributes are good candidate determinants of fecundity and mating success. The sexual selection gradient for one of these traits (e.g., body size) in males could then be estimated as the partial regression of mating success on body size holding the other traits constant. Likewise, the fecundity selection gradient for males could be estimated as the partial regression of fecundity on body size holding the other traits constant. Similar estimates could be made for the females. The selection coefficients that we have estimated are for a single reproductive season and are based on the supposition that the same partial regression slopes prevail at all ages.

Tests for assortative mating. The trait measurements on males and females can also be used to test for assortative mating. One simple test is to compute the correlation between the values of the same attribute of mating partners (e.g., the correlation between the body size of a male and the body size of a female that bore his progeny). A more powerful approach is to use canonical correlation analysis to analyze all the traits at once (Harris, 1975). For some genetic interpretations it would be informative to compute weighted correlations in which the data points represented by each male and female pair that produced progeny are weighted by the number of offspring that they produced.

Tests for inbreeding are conceivable but probably impractical. The issue of inbreeding arises most urgently in very small populations such as the European Adder population studied by T. Madsen and colleagues in southern Sweden (Madsen et al., 1992). In such populations one might wish to know the pedigrees of mating partners so that the degree of inbreeding can be established. Unfortunately, although DNA fingerprints can often be used for paternity assignment (if fingerprints are available for all potential fathers) it is unlikely that the technique will yield unambiguous determinations of more distant relationships (Lynch, 1988).

Estimation of genetic parameters. It would be possible to estimate such genetic parameters as genetic variance and covariance, heritability and genetic correlation if traits are scored in offspring as well as in their parents (Falconer, 1989; Brodie and Garland, Chap. 8, this volume). Unless the age of parents is known and a very large sample is available, the best course is to focus on traits that do not change with age (e.g., meristic traits such as scale counts). Beatson (1976) and Arnold (1988), for example, provide some examples of data analysis.

While a number of potential research protocols come to mind, we favor an approach that takes advantage of the rise of genetic methods to assign paternity, an approach that is revolutionizing behavioral ecology and sociobiology (Burke, 1989). We do not dismiss continued focus upon behavioral, physiological, and other dependent measures as well, however. Indeed, as our encounter rate models noted above should suggest, we value and recommend such approaches as well. The ideal situation for future studies, to our minds, would be to attempt to integrate diverse approaches formally, as we have attempted to argue through the theoretical rationale we have presented in the previous sections. In the end, it is our hope that such integration will facilitate general comparison.

Benchmark Studies of Snake Mating Systems

Based upon the foregoing, the reader might incorrectly assume that little of worth has been done on mating systems and sexual selection in snakes. This is hardly the case. Our goals thus far in this chapter have been to outline some new approaches to the study of relevant phenomena, approaches that hold some potential for integrating the analysis of (1) dynamic sexual selection forces and (2) pattern and variation in snake mating systems.

Our goal in this section, however, is to touch upon some key studies of snake mating system-related phenomena that have been undertaken. Though work in this area really has taken off only in the past few years, some of it is substantive. Seigel et al. (1987) review most relevant studies through the mid-1980s.

European Adder

The European Adder (*Vipera berus*) is perhaps the best studied snake with respect to its mating systems in nature. Many of the traits (or variables) that we have already indicated as important to understanding mating systems have been described, including data on geographical variation in the timing of mating (Viitanen, 1967; Prestt, 1971), various aspects of the reproductive biology of both sexes

(Volsø, 1944; Andrén and Nilson, 1981, 1983; Nilson, 1981; Andrén, 1982a,b; Saint Giron, 1982), multiple paternity (Stille et al., 1986), mate-searching and site(s) of mating (Viitanen, 1967; Prestt, 1971; Andrén, 1986; Saint Giron et al., 1989), mate competition among males (Kelleway, 1982; Andrén, 1986; Nilson and Andrén, 1982), life-history variables (Viitanen, 1967; Prestt, 1971; Andrén and Nilson, 1983), important aspects of natural history and the life cycle, such as seasonal movements and habitat selection (Viitanen, 1967; Prestt, 1971), predation (Andrén and Nilson, 1981), and foraging biology (Andrén, 1982b; Andrén and Nilson, 1983).

European Adders generally spend winters in communal dens and emerge in the spring, with adult males emerging prior to adult females (Viitanen, 1967; Prestt, 1971; Andrén, 1986; Madsen, 1988). Males disperse to areas termed "basking spots" (Viitanen, 1967), which are located only short distances from den sites. Males appear to select a particular individual basking spot where they will remain, on average, for several weeks (Viitanen, 1967). Foraging does not occur at this time. During the so-called basking period, males become reproductively competent (i.e., spermatozoa are present in the ductus deferens) and a complete skin shedding cycle occurs. After molting, males move a short distance to "mating areas," probably hotspots in our lexicon (see Bradbury et al., 1986), where receptive females reside and tend to cluster. Male fighting for priority access to females then occurs (Prestt, 1971; Madsen, 1988; Madsen et al., in press). The mating period lasts about a month, and both males (Viitanen, 1967; Prestt, 1971) and females (Stille et al., 1986) are known to engage in multiple matings with different individuals. Subsequent to the mating period, both sexes move to summer foraging grounds. At the end of the season they return to the wintering den sites.

Recent work on the European Adder by Madsen and colleagues (Madsen and Shine, 1992, 1993; in press; Madsen et al., 1992, in press; see Shine, this volume) has been quite successful in connecting key traits to mating success, a prime goal in integrating mating systems and selection theory (Duvall et al., 1992; Arnold and Duvall, 1993; Fig. 5.5). These studies have begun to provide the type of information we envision to be necessary to comprehend the accurate structure of mating systems. Importantly, their work also has provided insight into other general problems in animal reproductive biology, such as functions of multiple mating in females (Madsen et al., 1992).

Work on the European Adder by Madsen and colleagues also has revealed a number of insights into key determinants of mating success in males (Madsen and Shine, 1993, in press; Madsen et al., in press). Male-male combat is important in gaining access to receptive females, and larger males almost always win fights. Smaller (and

likely younger) males generally do not engage in fights. These smaller males, however, have been observed to wait nearby (i.e., satellite tactics?) and return to females after rivals have departed. Of 148 observed matings, smaller males achieved 15 (10%) of the total.

North American Rattlesnakes

Rattlesnakes (*Crotalus* and *Sistrurus*) represent a group for which there exists an abundance of biological information on most aspects of their life cycles, as well as natural and life histories (Gloyd, 1940; Klauber, 1972; Campbell and Lamar, 1989; Campbell and Brodie, 1992; Ernst, 1992). Surprisingly, few studies provide information on the structure of mating systems (see Duvall et al., 1992; Schuett, 1992). There are, however, a number of studies on rattlesnakes that have been successful in collecting some data of the type important to describing and comprehending mating systems (Fitch, 1949, 1970; Landreth, 1973; Reinert, 1981; Diller and Wallace, 1984; Gannon and Secoy, 1984; Jacob et al., 1987; Macartney and Gregory, 1988; Reinert and Zappalorti, 1988; Brown, 1991, 1992; Brown and Lillywhite, 1992; Martin, 1992; Secor, 1992).

We will focus our discussion on a long-term and intensive study of free-ranging Prairie Rattlesnake (*Crotalus viridis viridis*) populations in the Red Desert (Haystack Mountains) of south-central Wyoming. Work by Duvall and colleagues on these populations has generated information on seasonal movements and space use patterns (Duvall et al., 1985; Graves and Duvall, 1990; King and Duvall, 1990), foraging ecology (Duvall et al., 1985, 1990; Brown, 1990), reproduction and social structure (Duvall et al., 1985, 1992; Graves et al., 1986; King and Duvall, 1990; Hayes et al., 1992; Graves and Duvall, 1993; Schuett et al., in press), and mating systems (Graves and Duvall, 1990; King and Duvall, 1990; Duvall et al., 1992; Duvall and Schuett, in review).

Shortly after adult Prairie Rattlesnakes emerge from dens in spring, they initiate long-distance (up to ca. 5 km from den sites) migrations away from dens in search of preferred prey in summer activity ranges (Duvall et al., 1985, 1990). Unlike the European Adder (see above), mating and shedding never have been observed to occur in spring near den sites when both sexes are thus clumped and in close physical proximity. Rather, in midsummer, when individuals of both sexes are widely dispersed, males begin prolonged mate searching activities. When receptive females are located, perhaps by pheromone trails produced by females (see Ford, 1986), males will accompany and attempt to court females for 2–4 days prior to actual copulation. Rarely will more than one male locate a female simultane-

ously; thus, male-male fights are uncommon. The period of mating is ca. 6-8 weeks in duration, usually ending by late August. During late summer and early fall, both sexes return to overwintering dens.

Although most of our preliminary results (Duvall and Schuett, in review) are presented in Duvall et al. (1992), a few additional points can be made here. First, the narrow sense mating system we have observed in the Red Desert is prolonged mate-searching polygyny, with most males failing to find even a single female to mate with in a season. Almost all females, conversely, are mated. Of interest (but not surprising), male body size does not predict mate location success. Rather, a number of movement- and orientation-related traits are associated with mate location success. Given the extremely male-biased OSR and/or the unpredictable, sparse, and clustered distribution of females at the onset of the mating season, it was expected that movement and not body-size factors per se would be more important (Duvall et al., 1989; Mintzer et al., 1993; Duvall et al., in review). In due course, we intend to apply DNA fingerprinting methodologies in future studies, such as those described above, so as to gain a better understanding of sexual selection and microevolutionary response to selection, factors that will be critical to an improved understanding of Prairie Rattlesnake mating systems.

North American Copperhead

Autecological study of the Copperhead, *Agkistrodon contortrix*, by Fitch (1960) has provided a wealth of data on various aspects of the natural and life history of this viperid snake, including much information relevant to mating systems (e.g., seasonal activity and movements, timing and location of mating, life-history traits).

Inspired by Fitch's (1960) field work and Carpenter's (1984) lab work, Schuett and his colleagues have investigated various aspects of this snake's reproductive biology in the laboratory, including analysis of sperm storage (Schuett, 1982, 1992), courtship (Schuett and Gillingham, 1988), male competitive tactics (Gillingham, 1987; Schuett and Gillingham, 1986, 1989; Schuett, in manuscript), mate choice (Schuett and Duvall, in review; see below), and hormone cycles (Schuett et al., in manuscript).

In both nature and captivity (Fitch, 1960; Schuett, 1982; Schuett and Gillingham, 1986, 1988), Copperheads exhibit two distinctive periods of mating: the first occurs in late summer or early fall, and the second in spring (Schuett, 1992). Captive individuals of both sexes will mate in either one or both periods, and females can exhibit multiple paternity within single litters (Schuett and Gillingham, 1986). Male fighting (Fig. 5.6) can occur for priority access to females

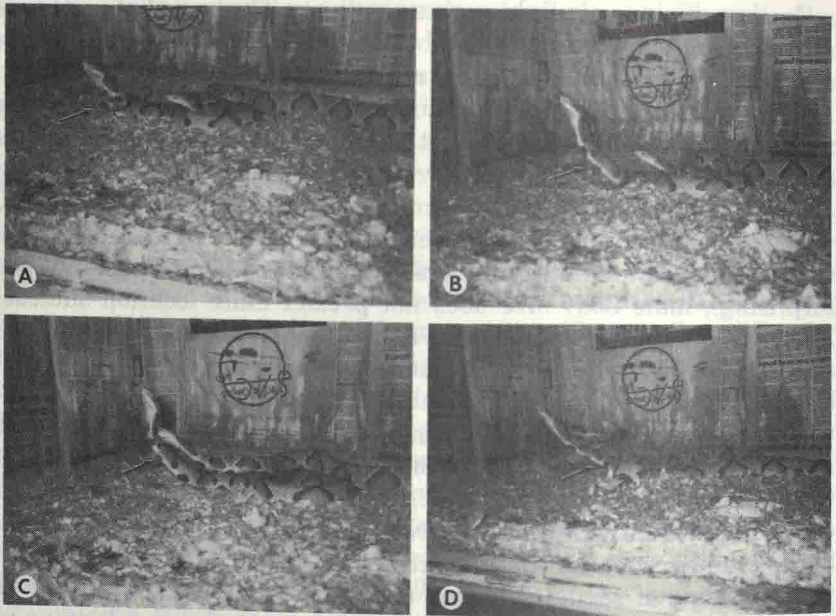


Figure 5.6 Sequence of fighting behavior in two captive male Copperheads (*Agkistrodon contortrix*): (A) approach and initial challenge displays; (B) both males in vertical posture (*sway*)—male in foreground is in the process of *hooking*; (C) initial phase of *entwinement*; (D) final phase of *entwinement* where separation will occur shortly thereafter (from Schuett, unpublished). See Schuett and Gillingham (1989) for a detailed description and analysis of the behavioral units and acts comprising fighting. See text for further details.

(Schuett and Gillingham, 1989; Schuett, in manuscript). Recently completed work on fighting dynamics (Schuett, in manuscript) has provided further insight into the determinants of agonism and mating success. Significantly, but not unexpectedly, body size (as measured by snout-vent length, SVL) was found to be an important determinant in winning staged fights. When SVL differences were 8–10%, larger males always won fights (Schuett and Gillingham, 1989; Madsen et al., in press; Schuett, in manuscript). Perhaps one of the most interesting findings was that losses in prior fights had a significant effect on subsequent fighting ability. In cases where contest losers were tested for fighting ability 24 h after a fight, and when paired with either the same male or a different male of the same SVL, prior losers never exhibited challenge displays and thus never engaged conspecifics in fighting. Even in cases where prior losers were tested at 24 h after a fight with males of smaller size (8–10% difference in SVL), again losers never challenged or fought. Thus it can be concluded that negative prior agonistic experience (i.e., losing fights) can override the normal positive influence of body size. In

order to begin looking at the physiological mechanism(s) mediating winning and losing fights, Schuett et al. (in manuscript) have begun working on the effect of agonistic experience on circulating levels of testosterone and corticosterone.

Female mate choice. Schuett and Duvall (in review) have discovered an unusual type of female choice in the Copperhead, *Agkistrodon contortrix*, that has not been documented in any vertebrate. During a study of the determinants of fighting success in males, as described above, it was found that females may select for male quality by mimicking key behavioral acts characteristic of male combat, which may in turn facilitate female discrimination between prior winners and losers of fights. Specifically, it was found that, when males initiated courtship, most females lifted their heads from the substrate, sometimes quite dramatically (Fig. 5.7), in response to tactile stimuli (e.g., chin-rubbing) derived from the male. Head-lifting by females was very similar in form to head-lifting which comprised the initial stages of the "challenge display" typical of males (compare Figs. 5.6 and 5.7; cf., Schuett and Gillingham, 1988, 1989). Males often responded to head-lifting with a challenge display of their own. Even so, male-female fights never were observed, and all females that exhibited head-lifting resumed pre-courtship postures within several minutes.

Interestingly, when a receptive female is present in the test arena, the loser of a staged fight between two males attempts neither further fighting with the winning male nor courtship with the female. The latter also holds even when the winning male is removed from the arena, or when the loser is placed into a novel arena with a different receptive female (Schuett, in manuscript). It also was observed that almost any action on the part of females at these times caused the loser to retreat.

It thus appears that female Copperheads may mimic an important component of ritualized male combat, so as to facilitate the discrimination of male fighting ability and perhaps quality.

North American Garter Snakes

A multitude of field and laboratory studies have been done on North American Garter Snakes (*Thamnophis*), far more than can be described here. Several provide detailed information relevant to mating systems analyses (cf., Ford, 1986). The best studied taxon in this respect is the Red-Sided Garter Snake (*Thamnophis sirtalis parietalis*) of the Interlake region of Manitoba, Canada (see Crews, 1992; Halpern, 1992; Mason, 1992; Moore and Lindzey, 1992; Whittier and Tokarz, 1992, for the essential references).

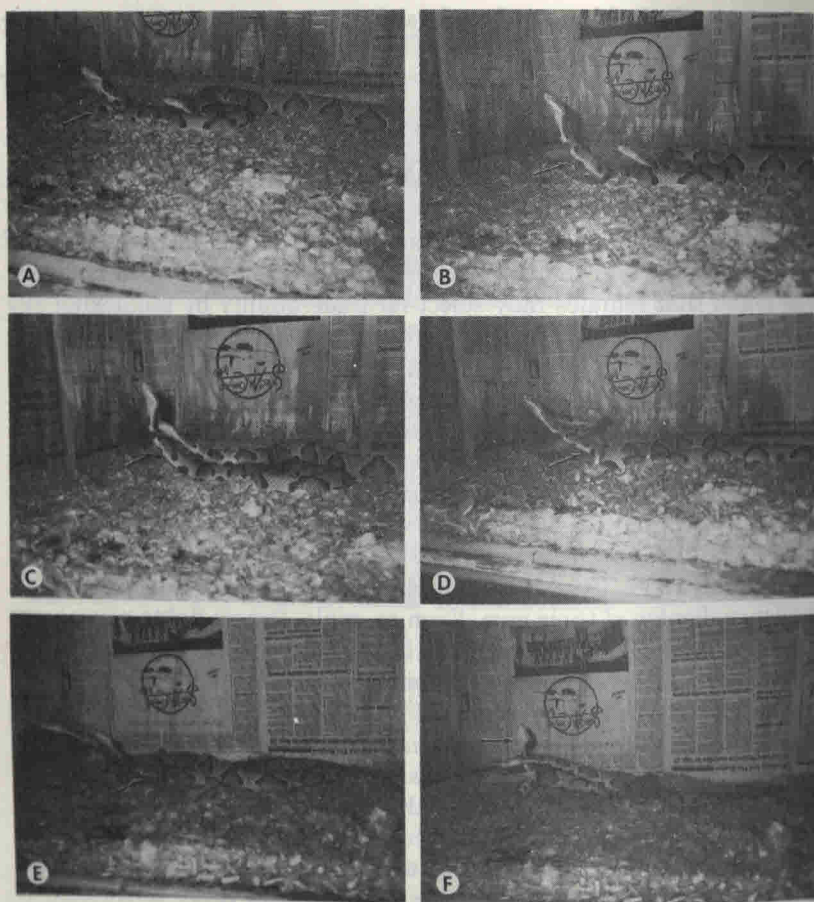


Figure 5.7 Mate choice by male mimicry in a female Copperhead (*Agkistrodon contortrix*): (A) the male approaching phase of courtship and the female (see arrow) exhibiting the initial postures resembling the *challenge display* of fighting males; (B) the female continues to exhibit the challenge display during courtship, and the male has temporarily ceased courtship; (C) the female assumes an even more distinctive vertical posture, and the male continues courtship; (D) the male responds to the female's display by initiating the challenge display; (E) the female in process of terminating her display and the male resuming courtship; (F) the male is moving back from female and initiates a challenge display (from Schuett and Duvall, in review). See text for further details.

In populations of Red-Sided Garter Snakes from Manitoba, explosive mating assemblages (e.g., "mating balls") can occur on warm days in the spring when most males have already emerged and females are just beginning to do so (Gardner, 1955; Gregory, 1974; cf., Graves and Duvall, 1990). Dozens, sometimes hundreds, of males and just a handful of females may comprise an individual explosive mating ball, or scramble. Determinants of male mating success are not

yet fully known, though male body size does not seem to be important (Joy and Crews, 1985, 1988; but cf., Madsen and Shine, in press). During the following coitus, which is fairly brief (5–15 min), copulatory materials are inserted and congeal in the female's reproductive tract, sometimes extruding from the cloaca (Devine, 1977, 1984). Copulatory plugs may enforce chastity and first-male advantage, and likely represent a form of mate-guarding (Ross and Crews, 1977). Contrary to some earlier views, multiple matings by females probably are common, and mating is not confined only to the spring (Whittier and Crews, 1986; Whittier and Tokarz, 1992). (Evidence for late-summer mating derives from females with copulatory plugs and/or sperm in the caudal regions of their reproductive tract later in the season.) In other populations of *T. sirtalis*, males have been observed to mate with multiple females, and mixed paternity has been verified (Gibson and Falls, 1975; Schwartz et al., 1989).

The seemingly obligate use of limited den sites in winter and the high densities of snakes that occupy them probably have been important selective factors in shaping the mating systems of these populations (Gregory, 1982, 1984). Although behavioral observations are limited, even late-summer mating activities might be influenced by migration episodes to the dens (P. Gregory, personal communication). Hopefully, future work on Interlake populations will include (1) investigations of the late-summer mating activities of larger samples of individuals and (2) analyses of DNA fingerprints of likewise large samples of individual neonates comprising litters. Such data could facilitate greatly analyses of the local mating system and dynamic sexual selection forces (Arnold and Duvall, 1993; see below).

Female mimicry recently has been described by Mason and Crews (1985) as an alternative mating tactic in the Red-Sided Garter Snake. In this case, a small fraction of males in the population, referred to as "she-males," mimic the courtship pheromones of females, attracting other males who thus waste their courtship efforts. Mason and Crews (1985) also determined that she-males not only are reproductively competent, but, in fact, mate more frequently with females than do normal males. In conclusion (p. 60), they argue that the "advantage to the she-male's attractiveness thus lies in an ability to gain a better position in the mating ball by confusing other males."

Male choice in snakes. Female garter snakes, like many other squamate reptiles, exhibit a well-known and strong positive association between increasing body size during growth and increased clutch or litter size (Duvall et al., 1982). Thus, to the extent that appropriate ecological and phylogenetic constraints apply, males should choose the largest, sexually mature female conspecifics with which to mate.

This has, in fact, been observed by several different investigators (Gregory, 1974; Hawley and Aleksyuk, 1976; Garstka and Crews, 1985). As yet, however, no one has considered how these patterns may have affected sexual selection forces acting on females. Though age-body-size covariance would have to be handled appropriately, the scheme we propose at the outset of this chapter (Arnold and Duvall, 1993) could be used to analyze this interesting problem quantitatively. Much more could be done with it.

Australian Diamond Python

The work of Slip and Shine (1988a,b,c,d,e; Shine, 1991, 1992; this volume) on the natural history of the Diamond Python, *Morelia spilota spilota*, is particularly important in that it represents the only published study of the mating system of a free-ranging boid (Slip and Shine, 1988a; Shine, 1992), and one of the best documents of habitat use, thermal ecology, and mating frequency in any wild snake. Using radiotelemetry, Slip and Shine (1988a), documented courtship and mating behaviors of *Morelia s. spilota* from 1982 to 1984. They found that during the mating season (spring; late September to early November) it was not uncommon for individual receptive females to be trailed, accompanied, and courted by multiple males (Shine, 1991). Females engaged in multiple matings with the same and/or different males, sometimes within very brief periods (e.g., 1–2 days). Interestingly, during periods when multiple males (e.g., 2–4 individuals) accompanied individual females, male combat (see Covacevich, 1975) was never observed. Slip and Shine (1988a) hypothesized that multiple-male accompaniment and the lack of male agonism resulted from (1) low numbers of receptive females, (2) a low likelihood of males locating additional receptive females, and (3) potential high costs of fighting. Although advantages of multiple mating by female snakes remains somewhat unresolved (Schuett, 1992; but see Madsen et al., 1992), Slip and Shine (1988a) suggest that potential advantages may include (1) ensuring sufficient quantities of viable sperm, and (2) reducing survival and/or energetic costs by not rejecting courting males when courtship and mating are low-risk activities (Gibson and Falls, 1975; but see Devine, 1984). Moreover, although they suggest that courtship and mating may attract predators, no such evidence is presented. Based upon correlated evolution alone, however, some degree of female multiple mating should not be unexpected (Lande, 1979; Lande and Arnold, 1983; Halliday and Arnold, 1987), particularly in light of the strong sexual selection for multiple mating likely acting on most male snakes (see polygyny rationale for most snakes in preceding sections).

Additional work on mating systems of Diamond Pythons and their close relatives, the Carpet Pythons, is in progress (Shine, 1992; R. Shine, personal communication). One goal is to identify proximate factors that result in the presence of fighting among Carpet Pythons and its absence among Diamond Pythons. The mating system of another species of python (*Liasis fuscus*) from tropical Australia (near Humpty Doo, Northern Territory) is currently being investigated by Shine and colleagues as well (Shine, 1991, 1992). Indeed, Shine and colleagues have examined mating systems and related phenomena in a number of other Australian snakes (Shine, 1977a,b, 1986, 1991; Shine et al., 1981).

Summary and Future Research

Clearly, work has only just begun in the area of snake mating systems and sexual selection. If the few studies that have been done so far are any indication of what is to come, however, the future looks bright indeed. In this spirit, herein we have attempted to present formal microevolutionary models that may facilitate future research, by showing interconnections between various bodies of relevant theory and at least a few empirical directions. We also have attempted to focus on some of the benchmark studies that have been done, that address key features of relevant microevolutionary processes. Another hope is that molecular genetic techniques such as DNA fingerprinting find a home in analyses of snake mating systems and sexual selection, especially in light of the power such approaches bring to the game of evolutionary behavioral research.

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